DISTRIBUTIONS OF TYPES:

The holotype is deposited in the San Diego Museum of Natural History, San Diego, California, Number 45,924. Paratypes I and II and hypotype I are in the private collection of the senior author.

NAME:

This new species of Trivia is named in honor of Elsie M. Chace for her long-standing interest in conchology and for the unstinting help which she has given the authors over the many years they have known her.

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Further Remarks on the Interpretation of the Mollusca

by

W. Patrick Milburn

(Plate 8)

Last year, in a paper titled, "Neopilina and the interpretation of the Mollusca" (Milburn, 1959), I made an attempt to outline the relationships of the classes of mollusks based in the largest part on gill characteristics. A particular orientation towards classification and the recognition of relationships was developed taking the point of view that all of our systems and phylogenies should always be recognized to be constructs made from the available data. Since that discussion, further study has forced correction of some of the propositions and has reinforced others. Both the correction and the reinforcement have made more clear the problems involved in these studies. Further, additional study of procedure has led to ways of improving these constructs. The discussion will concern the topics in this order: 1) the correction of relationships and its importance; 2) the reinforcement of the previous views and its significance; and 3) the suggested improvements in the methods of making these constructs.

I. Corrections of Postulated Relationships.

Without any substantial evidence, the conclusion was stated that "Neopilina is flat and from a form like this it is easy, at least in principle, to derive the chitons and solenogastres" (Milburn, l. c., p. 26). This was a contradiction of the methodology, and it is now clear that only in principle would it be possible to derive these groups from something like Neopilina. Further evidence suggests that not all of its characters are exceedingly primitive.

The error of my previous conclusion was made clear to me in a discussion with Drs. Donald P. Abbott and C. M. Yonge in which it was suggested that the ancestral mollusk may have been much more primitive than Neopilina. In support of this, it was pointed out that the state corresponding to a veliger in the chiton has several shell plates right from the start and never a single plate as in the higher mollusks. The unlikelihood of a single shell being broken transversely into eight plates was also

mentioned.

Investigating this possibility, a review of the characters of Neopilina in the Galathea Report was found to strongly support the position of the above discussion. Neopilina differs from chitons and is similar to the higher mollusks in 1) possessing a single shell plate with growth on the edge (Lemche, 1959, p. 64); 2) in possessing a larval shell similar in some respects to that of gastropods (Lemche, 1957; Lemche, 1959, p. 64); and 3) in having a shell of three distinct shell layers, a periostracum, a prismatic and a nacreous layer (Lemche, 1957, p. 64). The chitons are quite different in 1) having the shell of eight plates growing by transverse growth; and 2) having the shell of two shell layers, a tegmentum, and an articulamentum. [After the reading of this paper at the thirteenth convention of AMU-PD, it was mentioned to me that some new work suggests that one of the layers of a chiton's shell may actually consist of two layers; I have not yet seen this work but the two layers are certainly not as clearly marked as in higher mollusks.] Finally, 3) in having a larval shell composed of several plates (Heath, 1899). A comparison of the veligers of these forms (Figure 1) demonstrates the similarities of Neopilina, at least in the shell, to the veliger and its differences from the chiton larva. Further, Neopilina seems similar to bivalves and gastropods in having its lateral nerve cords meeting below the rectum (Lemche, 1959, p. 50).

Thus, quite differently from my suggestion of last year, these data suggest two major concentrations of characters, the Amphineuran forms and the higher mollusks plus the Monoplacophora. Although I was not aware of it at the writing of last year's paper, such a division as just proposed had already been suggested long ago. Grobben (1905) may have been the first to divide the mollusks into these groups, calling them Amphineura and Conchifera, which, however, he considered classes (l. c., p. 586). Grobben credits Gegenbauer with the proposal for the unification of the gastropods, scaphopods, bivalves, and cephalopods in the Conchifera (l. c., p. 591). In 1926 Naef raised Grobben's classes to subphyla (Naef, 1927, p. 87).

Lemche attacks this division into Amphineura and Conchifera on the grounds that Neopilina has both the nervous system of the Amphineura and the shell of the Conchifera, thus breaking the principal characters (Lemche, 1959, p. 68). This criticism of the definition seems well taken, as does the criticism of uniting all of the "conchiferans" into a class. However, Lemche's conclusion that we should regard all of these groups as independent classes arising from some common ancestor is not consistent with the data he has given. Clearly, the Monoplacophora, Cephalopoda, Gastropoda, Scaphopoda, and Pelecypoda form a supergroup based on at least the characters of the distinctly three-layered shell, the similarities of the larval shell, perhaps the features of the posterior nervous system, and probably several more. The characters as stated for the Conchifera may have to be revised, but this division still seems to be supported, with the Monoplacophora not being the most primitive group of mollusks but rather being the group of "conchiferan" mollusks with the most primitive characters.

Whether or not the solenogastres will belong in the subphylum with chitons cannot yet be stated. They both have one set of kidneys, but the significance of this is difficult to assess since this seems to have developed independently in both the dibranchiate cephalopods and in the gastropoda-pelecypoda group (Morton, 1958, p. 65). Moreover, the kidney structure is very different in solenogastres and chitons so that they may well represent separate lines. In solenogastres, the two gonads are separate and empty through the kidneys out a single pore. In chitons the gonads are fused into one which dumps out of two pores separately from the kidneys (Goodrich, 1946, p. 336). In solenogastres the nervous system seems somewhat more complex and condensed than in chitons. Clearly, more information is needed, particularly of development, if a decision is to be reached. If it finally looks as though these groups ought to be separated, I hope that names are chosen which will agree with Conchifera better than Amphineura does as far as some similar character is concerned.

Interestingly, gill structure does not give the help at this level that it does when considering the relationships among the classes of higher mollusks. In chitons (Yonge, 1939, p. 378) and in Neopilina (Lemche, 1959, pl. 46, fig. 143) the water flows first over the refreshed blood as in gastropods and pelecypods. They are different from these more advanced groups in lacking gill-bars. In the cephalopods the condition is quite different, with gill-bars present (opposite in orientation to the gastropod-pelecypod scheme) and the water flows first over the de-

pleted blood (Milburn, 1959, p. 27). Evidently, the condition in Neopilina and chitons represents the primitive condition, that of the gastropods and pelecypods the addition of gill-bars, and that of the cephalopods a reorientation and addition of gill-bars.

In the previous paper, the placing of the Monoplacophora as ancestral was clearly caused by a conception that Neopilina is primitive. This was a serious logical error which ran in direct contradiction to the method outlined for formulating constructs. We are all too much in danger of being overly impressed by the idea of the primitive. It may lead us to continually recognize those features that are of a primitive nature, while not recognizing those features that are advanced or divergent. The point should be emphasized that we should not regard any form as totally primitive, even if it possessed a majority of primitive traits. All organisms have diverged to some extent. If we do not take care in our thinking, we can slip into a kind of Idealism. Doubtless, Neopilina retains many of the primitive features of the phylum, but its similarities to the "conchiferan" forms also indicate how far in the differentiation of the phylum the primitive gill, segmentation and nervous system were retained.

II. Reinforcement of Previous Conclusions.

In the previous paper, I suggested, on the basis of gill structure, that the gastropods and pelecypods belonged in the same supergroup, which should also contain the scaphopods (Milburn, l. c., p. 25). It is interesting to note that Grobben had set up the Prorhipidoglossomorpha in 1905 (Grobben, l. c., p. 591) and Naef the Heteroneura in 1926 to contain these three groups in opposition to the cephalopods (Naef, l. c., p. 88). Besides having the water flowing first over the refreshed blood (when gills are present) [Milburn, l. c., p. 26], the following of Naef's characters also seem rather strong (Naef, l. c., p. 89): 1) a primary union of the pleural, cerebral, and pedal ganglia; 2) the visceral commissure being up under the hindgut and in the groove between the head and the roof of the mantle cavity; 3) the reduction of the anal complex to one segment, opposed to two segments in the cephalopod Nautilus; and 4) the release of the sex products through the kidneys. (This last character is true in gastropods, scaphopods, and protobranch and filibranch pelecypods but not in the eulamellibranchs [Yonge, l. c., p. 326].)

A more exact position of the scaphopods is not certain. Naef mentions that their nervous system is similar to pelecypods, particularly in having a lengthening of the cerebro- and pleural pedal connective (Naef, l. c., p. 64). The larval shell is a cap-like plate in scaphopods and pelecypods (Schrock & Twenhofel, 1953, p. 494). Plate (1922, p. 451) mentions that they are close to the primitive gastropods in that they still have a head with a mouth tube, a pharynx with radula and jaws, a single shell, and an unpaired gonad with discharge [through the right kidney]. They thus share important characters with both gastropods and pelecypods, and it is not clear to which of these two groups they are more closely allied, if, indeed, to either.

If these relationships and clusters of characters are placed in a taxonomy, the form is as follows:

Phylum Mollusca
- subphylum Amphineura (perhaps separate subphyla will be required for chitons and solenogastres)
  - Class Polyplacophora - chitons
  - Class Aplacophora - solenogastres
- subphylum Conchifera (Gengenbauer, Grobben, Naef)
  - superclass ******** (name not proposed)
    - Class Monoplacophora
  - superclass ******** (the Prorhipidoglossomorpha was not for a superclass; the Heteroneura also does not seem to have been clearly proposed. There is a chance, then, that a descriptive name can be formed for this group)
    - Class Gastropoda
    - Class Scaphopoda
  - superclass ******** (name not proposed)
    - Class Cephalopoda

It is hoped that helpful, descriptive names for the superclasses and for the subphyla of chitons and solenogastres (if they are sufficiently distinct) will be proposed and not vague terms or terms reflecting some contrived phylogenetic speculation. The suggested relationship of the classes is indicated in figure II, plotted against the fossil record of the classes (Nicol, Desbourough, & Solliday, 1959).

III. Improvements in the Method.

It is my feeling that all of the products of the human mind are symbolic constructs of one sort or another. Accordingly, that is certainly the case with systematics. Further, it is my feeling that most classifications are in reality based on a large number of characters, included in the total form perceived by the person, whether these are verbalized or even recognized. It is perhaps not clear that this "totalizing" is going on at the level of genus or family, and it is not necessary that it be recognized there. When relationships are very distant or obscure so that the mind cannot easily derive the characters, it does become necessary to verbalize all of the characters so that we may formulate classifications and perceive relationships. As an additional gain, by listing all of the available evidence, the process becomes more objective, more verifiable, and we gain a much greater ability to predict since we will have a greater body of common characters.

As we have seen, the higher taxonomy of these German zoologists anticipated the evidence derived from gill-structure. Their work was not generally adopted, particularly in the English-speaking part of the world. Perhaps it was still too far from the degree of certainty hoped for by taxonomists.

We may ask, "How many characters must we use in our constructions to gain a high enough level of probability to institute proper subphyla?" Michener and Sokal (1957, p. 160), who have applied mathematical probability to a group of insects suggest that the number of characters, to be reliable, should not be less, and need not be more, than 60. Many characters can be taken from each system and the results totaled by a desk computer. Olson and Miller (1958, p. 58) have suggested that statistical methods be utilized to analyze the correlation of characters in an organ system or region of the body. This could prove of aid in evaluating characters and in providing developmental characters. These methods offer a great deal of hope and lead to the proposal that such mathematical investigations be attempted for the Mollusca. Not only might this lead to a reliable set of subphyla and superclasses for the phylum, but this mode of analysis might well help us in analyzing the relationships within the Pelecypoda, Mesogastropoda, Opisthobranchia, and other groups.

The point deserves to be emphasized at this time that, even if statistical means are employed, this in no way detracts from the efforts of the taxonomist. He still must recognize characters and perceive relationships, even if the data is organized to help him. The task of classification is a creative, human endeavor, whether one uses large amounts of information or not. One is simply more certain of the result if a large number of characters are used.

Summary: 1) Neopilina, while possessing numerous primitive traits, seems to be less primitive in some respects than the chitons and to be related to the mollusks with a shell plate in three layers; 2) the character distribution of chitons and solenogastres is not yet certain, and two subphyla may be necessary for these groups; 3) the evidence suggests that a subphylum for the mollusks with a single larval shell and an adult shell in three layers divides naturally into three superclasses, one for the Monoplacophora, one for the Cephalopoda, and one for the Gastropoda, Pelecypoda, and Scaphopoda; 4) it is urged that statistical analyses of the characters of molluscan groups be carried out in order to clarify relationships and to increase our ability to make predictions.

Explanation of Plate 8

Figure 1: *Neopilina* larval shell compared with chiton larva and gastropod veliger.

Figure 1 a: Chiton trochophore (example of trochophore stage common to most mollusk groups)

Figure 1 b: Stage in chiton development corresponding to veliger indicating the developing eight shell plates [a and b from Heath]

Figure 1 c: Apical part of shell of *Neopilina* with larval shell [from Lemche, 1957]

Figure 1 d: Veliger of gastropod (*Crepidula*) [from Emily Reid]

Figure 2: Probable higher relationships of the classes of mollusks plotted against their record in time and indicating a possible "ancestral mollusk" [redrawn with modifications from Nicole et al.]

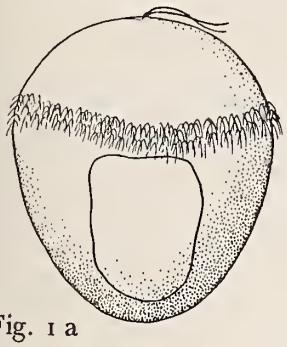


Fig. 1 a

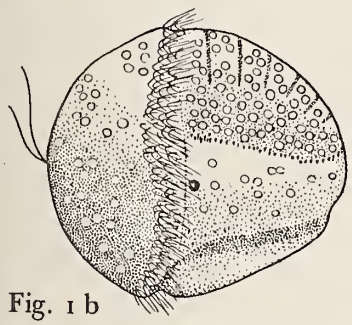
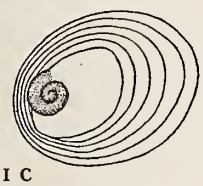


Fig. 1 b



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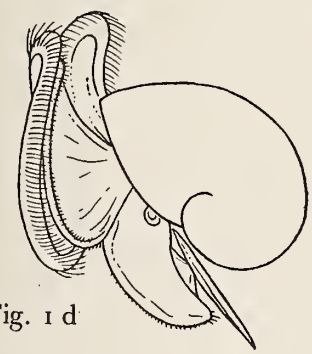

Fig. 1 d

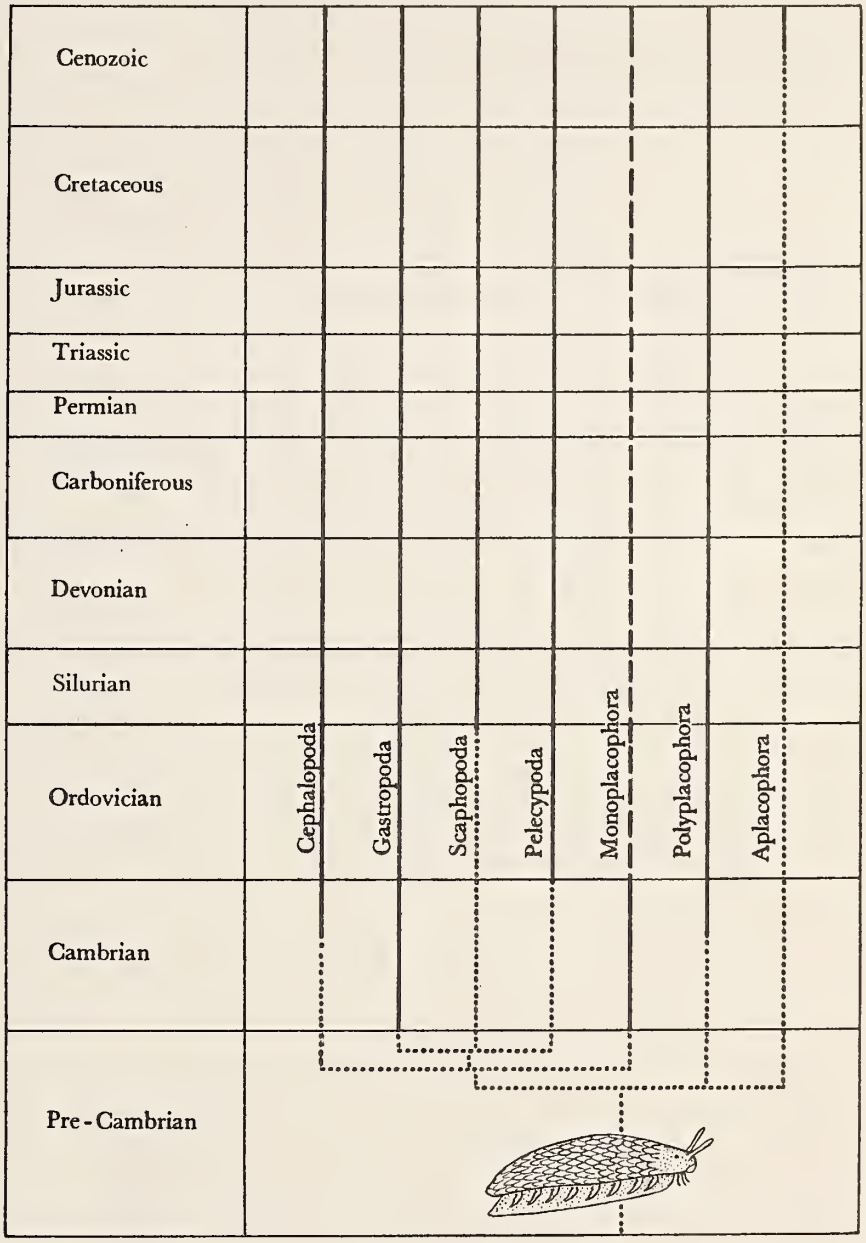

Figure 2

Explanation of markings:

Complete fossil record with or without recent examples. ——————

Gap in fossil record between fossils and recent examples. — — — — — —

Fossil record absent; relationships indicated represent a construct. ·····